E/CONF.39/C/443
2 Nov.1962
ORIGINAL : ENGLISH

UNITED NATIONS CONFERENCE
ON THE APPLICATION OF SCIENCE AND TECHNOLOGY
FOR THE BENEFIT OF THE LESS DEVELOPED AREAS

Agenda Item: C.4.1

United States of America

PRINCIPLES OF PLANT GENETICS AND THEIR USE IN INCREASING FOOD PRODUCTION

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PRINCIPLES OF PLANT GENETICS AND THEIR USE IN INCREASING FOOD PRODUCTION

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Introduction

1. Improved varieties of crop plants, developed by application of genetic principles, provide increases in total yield of food, feed or fiber; reduce production losses caused by diseases, insects and other hazards; improve nutritive and industrial values of the crops; facilitate introduction of the crop into new areas; and reduce production costs through greater efficiency of fertilizer usage, easier culture and harvest and adaptation to mechanization. Plant breeding provides short-term benefits from use of superior local seed sources or introduced varieties and long-term benefits through development of varieties specifically designed for local soil, climatic and use conditions. In less developed countries, improved varieties have the advantage of requiring, after the variety is developed, little capital outlay by the farmers. Furthermore, experience has shown that improved varieties lead the way to other improvements by the farmers in cultural practices, irrigation, fertilization, and disease and pest control.

Testing Indigenous Materials and Introductions

2. The first step in plant breeding is evaluation of already existing materials. These include such indigenous materials as local varieties, farmers' seed lots and natural stands, as well as varieties and collections from other areas of the world. These materials frequently enable the plant breeder to identify varieties that can be increased and distributed without further breeding work and to assess the characteristics of the crop which are most in need of improvement. Large differences among seed lots in different villages and among farmers' lots in the same village may be expected, and distribution of the best varieties can have an important impact within a short time on crop production in the country. For example, in Thailand approximately 40 rice varieties had been identified as standard government varieties. In an expanded breeding program these varieties were tested at several locations with the striking result that the best standard variety produced up to 80 percent more than the poorest. Recognizing that the varieties in these official trials represented only a small sample of the wealth of types among farmers' seed lots, 3000 "varieties" were collected from various parts of Thailand. After four years of testing, the best collected seed lots exceeded the superior standard variety by 16 to 40 percent at one location.

3. Another important potential source of "ready made" varieties which can be put to use quickly in the developing country is introduction of varieties from other areas of the world. Agro-climatic analogues exist between various countries, and varieties adapted in one country may in general be expected to be adapted in another with similar ecological conditions. The first varieties of cereal crops, clovers, alfalfa, soybeans and many other crops in the United States were direct introductions from Europe, the Near East and East Asia. Introductions have played an important part in "filling the gap" with useful varieties in many countries while the somewhat

slower formal breeding programs were developing specifically adapted superior varieties.

4. In postwar Europe the hybrid corn production program began on the foundation of certain U. S. hybrids several years before it could have been based on hybrids specifically bred for the various European conditions. In a like manner, U. S. maize hybrids were found to be superior in yield to desai corn in parts of India; although the difficulty of maintaining the inbreds and producing the single crosses made them unsuitable for Indian conditions, nevertheless their superiority helped to pave the way for the Indian Coordinated Maize Breeding Scheme and, here again, plant introduction played a key early role. The first four double cross hybrids, now being introduced only four years later, are from crosses involving, in various combinations, three inbreds of Indian origin, three from U. S. germplasm, and four of South American origin. These four hybrids produce yields of 122, 142, 151 and 153 percent of the best local strains in the areas for which they are released.

5. In the United States "World Collections" of wheat, oats, barley, corn, rice, soybeans, flax, alfalfa, and several other crops are maintained on a systematic basis. The plant breeder in a developing nation can tap this resource of germplasm by writing to the Agricultural Research Service, U. S. Department of Agriculture, or the United States A.I.D. Mission in his own country.

Plant Breeding Procedures

6. Once suitable breeding materials have been identified, the breeding objectives clarified, and, if possible, progress made on increasing and distributing "stop gap" varieties, a more formal plant breeding program can be initiated. There are three basic steps in plant breeding; namely, (a) finding or developing suitable populations within which effective selection can be practiced; (b) selection, including evaluation of the selections; and (c) use of the selections to produce varieties for distribution to the farmers.

Finding or Developing Populations for Selection

7. A suitable population for selection is one which has sufficient genetic variability and within which the genes desired in the new variety occur in high enough frequency to permit the recovery of combinations of them in populations of feasible size. The plant breeder is, in general, limited to the genes that are available in the populations which he has. Furthermore, frequencies of the desirable genes are important in the effectiveness with which the plant breeder can select for combinations of them. Although much progress can be made by selection in existing populations, particularly in the early stages of the breeding program, greatest ultimate progress can be expected by developing populations which have combinations of genes and gene frequencies which lead to most effective progress by selection. A number of breeding methods or mating systems are available. These include hybridization, inbreeding, backcrossing, recurrent selection, and reciprocal recurrent selection. These methods are treated in some detail in recent plant breeding textbooks, including those by Hayes, Immer and Smith; Elliott; Poehlman; and Allard.

8. Hybridization is the most powerful tool for creating source populations. The segregation and recombination that occur following hybridization result in extensive genetic variability, a prerequisite to successful selection. Controlled hybridization between parents of known performance has been used extensively in the more advanced breeding programs with the self-pollinated crops. In cross-pollinated crops, where genetic variability in natural populations is very high, controlled hybridization has been less essential. Nevertheless, hybridization between selected inbred lines of maize has been an effective means of producing new populations from which superior inbreds can be extracted. Intervarietal hybrids and crosses between

non-inbred clones have also been used in alfalfa, Hevea, cacao, fruit crops and other cross pollinators.

9. Inbreeding results in rapid increase in homozygosity and segregation of the population into lines with varying degrees of relationship to one another. In the naturally self-pollinated species, in which inbreeding by selfing occurs normally, populations which develop following hybridization consist, after a few generations, of predominantly homozygous plants. A practical level of homozygosity is reached by the F_5 to F_8 generations. Breeders of the self-pollinated species differ regarding steps to follow between hybridization and the point of relative homozygosity. Proponents of the pedigree method use visual selection of individual plants in each generation and of the progenies of these selected individuals in each succeeding generation. By F_5 to F_6, the remaining lines are but a small sample of the total genetic recombinations that would be found in a corresponding unselected population. Hopefully, this selected sample will have a substantially higher frequency of favorable genes than the unselected population. Proponents of the bulk method do not attempt to apply selection pressure on the population during the several generations between hybridization and the time of relative homozygosity. Shifts in gene frequency in such populations are the results of drift or natural selection. Selection by the plant breeder is started in F_6, F_7 or F_8. Neither the pedigree nor the bulk method is clearly superior in all circumstances. Choice of the time at which selection pressure should be applied depends upon a number of factors, including mode of inheritance of the most important characters, the facilities available to the plant breeder, and his knowledge and skill.

10. Inbreeding, usually by enforced self-pollination, is commonly used in the naturally cross-pollinated crops. The objectives are to (a) speed up increase in frequency of desirable genes and (b) to develop lines that can be reproduced from seed through successive generations of evaluation and subsequent use in the breeding program. Where selection for favorable genes can be effectively made on the basis of the individual plant or selfed progeny, inbreeding by selfing provides the most rapid method of obtaining lines that are homozygous for such genes. On the other hand, there is evidence that inbreeding with visual selection is relatively ineffective in raising the average frequencies of desirable genes for such characters as combining ability for yield. Because of the urgency for producing improved maize varieties as rapidly as possible, the first hybrids distributed in Mexico were produced from four S_1 lines. Use of lines inbred for additional generations resulted in more uniform hybrids but little improvement in yield over the hybrids was made from S_1 lines. Although there may be advantages in more inbreeding, it seems obvious that improved maize yields that can come from hybrids should not be delayed by a long inbreeding program.

11. Backcrossing results in a rapid and predictable shift of gene frequencies in the population, following hybridization, toward the genotype of the recurrent parent. When continued for sufficient generations, all plants of the population theoretically will have the same genotype as the recurrent parent except for genes from the non-recurrent parent retained by deliberate selection. Backcrossing is an appropriate tool when one of the parents is superior in a number of characteristics while the other parent is deficient in most. For example, results with rice in Colombia indicate that backcrossing may be expeditious in producing adapted varieties with resistance to the hoja blanca disease. Certain introduced varieties, including Bluebonnet 50, have proved to be superior varieties for use as recurrent parents.

12. Recurrent and reciprocal recurrent selection are effective methods of increasing desirable gene frequencies in populations while retaining a high level of heterozygosity and genetic variability. In this respect, these methods contrast with inbreeding where, through rapid progress toward homozygosity, genetic variability, and hence further progress through selection is rapidly reduced. Success with these procedures

has been reported in breeding maize, Melilotus officinalis and Lolium perenne. A major potentiality of recurrent selection for use in developing countries is that the new population developed at the end of each cycle may, if desired, be increased as a synthetic variety. Such a procedure is being used successfully in Colombia in development of improved synthetic varieties of maize.

Selection

13. Success in plant breeding, once suitable source populations are available, is dependent upon the effectiveness of selection. In order to maximize the effectiveness of selection, the plant breeder must seek to reduce the differential environmental effects to a minimum, relative to the genetic differences in the population. He has several means for doing this including (a) special measures for control of the environment and for insuring as nearly as possible uniform environments for all plants in the population, (b) appropriate experimental designs to reveal differences, control and measure error, and to provide a valid estimate of significance of the differences, and (c) use of selection units appropriate for the characters for which selections are made.

14. One of the simplest and frequently neglected methods for reducing environmental effects is by good cultural practices, good stands and uniform fertilization. These are inexpensive practices that are within the grasp of any plant breeder. The breeder of a crop cannot hope to be successful until he has learned how to grow the crop. Other steps to reduce environmental effects include special disease nurseries and controlled insect infestations in which uniform disease or insect distribution is fostered by various techniques. Finally, the breeder may find use for special facilities for control of photoperiod, light intensity, humidity and temperature in greenhouses or environment control rooms. Since much progress can be made in breeding by less expensive equipment, the plant breeder in the developing country usually will not require such equipment, at least for a number of years.

15. In the self-pollinated crops, in which the relatively homozygous selections are increased to become the varieties of commerce, the selection unit is normally the plant itself or its selfed progeny. In the cross-pollinated crops, on the other hand, the selections normally are used for development of synthetic or hybrid varieties. Since the selections are to be used in hybrid combinations, they usually may be evaluated most effectively in some kind of hybrid combination. The usefulness of tests for general and specific combining ability, the efficacy of early versus delayed testing, the most efficient tester parents to use, and other problems related to evaluation of selections are dealt with extensively in the plant breeding literature. The interested reader is referred to such books as Hayes, Immer and Smith and to many recent journal articles.

Use of Selections

16. In the naturally self-pollinated crops, selections usually are increased through successive generations to become the varieties of commerce. Exception to this is found in some crops, tomatoes for example, in which ease of producing hybrid seed and the relatively small amount of seed required make the use of F_1 hybrids feasible. In vegetatively propagated species, such as potatoes and sugar cane, the varieties used commercially are clones of the original selections. Selections, whether families, inbred lines or clones, of the normally cross-pollinated crops are used in the development of synthetic varieties or as parents of single, three-way or double-cross hybrid varieties.

17. The striking success of hybrid maize in the United States has focused attention of plant breeders on the potentialities of using maize hybrids in other areas of the world and of using hybrid varieties of other crops as well. Maize hybrids were introduced soon after the war in Eruope and much European maize production is now based on hybrids. Maize hybrids have also been developed and distributed for use in Mexico, Colombia, India, and several other countries. In Mexico, in 1960, a new maize hybrid, H-507, was released which yields 20 per cent more than the pre-

viously recommended hybrid, H-503, and about 35 per cent more than the best open-pollinated native varieties in the area. Yield increases of similar magnitude are being obtained from new maize hybrids in Colombia and in India.

18. Although the best hybrid varieties will yield more than the best synthetic varieties that can be produced, difficulties are frequently encountered in adequate scale production of hybrid seed. This is especially true in some developing countries where neither private nor public institutions are available for an orderly process of seed increase and distribution. In such situations, synthetic varieties of maize may prove to be an acceptable solution at least until the procedures for hybrid seed production on an adequate scale can be developed. Much of the improved maize seed used in Mexico is from advanced generations of double cross hybrids. These synthetics have approximately one-half the yield superiority over open-pollinated varieties that the hybrids have. Extensive breeding programs are in progress in Mexico and Colombia on the development of superior synthetics by combinations of several inbred lines and by recurrent selection. In other crops where hybrid seed is not readily produced, synthetic varieties are likewise the means for using selections. The development of synthetics in forage grasses and legumes has been very successful. Controlled hybridization between non-inbred clones has also been used in Central and South America in rubber and cacao.

Cooperation in Plant Breeding

19. Cooperation is one of the most important factors in a successful plant breeding program. This includes cooperation among scientists of different disciplines within the same organization and among scientists of the same discipline in different organizations, stations and countries.

20. Dr. H. K. Hayes, Emeritus Professor of Agronomy and Plant Genetics, University of Minesota, has at different times helped with development of plant breeding programs in China, Chile and The Philippines. In each case, he gave major emphasis to the development of cooperation among research workers and it is probable that this was the most permanent of the many contributions he made. The remarkable agricultural progress in Taiwan is, at least in part, attributable to excellent cooperative and coordinated research and development programs. This cooperation may well be a legacy of the understandings which Hayes helped the Chinese scientists reach on the mainland almost 30 years ago.

Seed Production and Distribution

21. Plant breeding does not contribute to increased food production until seed of the improved varieties are generally available to the farmers. Experience in many countries, including the United States, has shown that seed increase and distribution do not take care of themselves automatically. When small lots of seed of a new variety are distributed and there is no organized effort to guide further increases, the variety is soon lost or the seed becomes mixed with other types.

22. The procedures and organizations for orderly increase and distribution of seed of improved varieties vary considerably among countries. For varieties developed by public agencies, the usual procedure is for a government agency, frequently the plant breeding station, to maintain the "breeder seed" and to produce the "foundation seed". From this stage, procedures vary between the extremes of (a) having all seed of subsequent classes, which will be used by farmers for commercial planting, produced by private seed growers and (b) having all seed of subsequent classes produced and distributed by government seed farms. Any one system of seed production and distribution will not be best for all situations. Instead, the system used must be fitted to the needs and conditions of the country. Nevertheless, the following principles are suggested as guides in devising the seed production and distribution system:

(a) The breeder seed can best be maintained under the close supervision of the plant breeder who developed the variety.

(b) Reliable planting stock (foundation and registered seed) must be available in sufficient quantities for production of the seed that the farmer plants for his commercial crop. This requires some kind of organized program, either public or private.

(c) For production of large quantities of certified seed, private producers are usually more efficient than government seed farms.

(d) Government subsidy of the price of seed of improved varieties does not, in the long run, result in as much farmer acceptance of the improved varieties as when he must pay a premium price for the seed.

- (e) There is need for a certification program, by government or private agency, to insure maintenance of varietal identity and purity.

Special Methods of Breeding

23. Numerous special methods of breeding are available, including transfer of genes from related species, chromosome doubling, use of monosomic and nullisomics, and induction of mutations by radiation. Use of ionizing radiations and other mutagens has attracted the attention of plant breeders as a new tool. Enthusiasm has been particularly high in areas where conventional plant breeding is less well developed and where needs for increased food production are great. Mutation breeding has been grasped as a sort of magic carpet by which the plant breeder can hope to span, in a few years, the developments by conventional plant breeding in other areas during half a century. A quotation from a recent symposium is particularly relevant for less developed countries:

> "As a general rule, the plant breeder cannot afford to adopt it (mutation breeding) today as a breeding method. To do so will result in wasting the time and facilities so used. The plant breeder who studies mutation breeding must do so primarily to evaluate and develop the tool. Unless he has more than sufficient resources for plant breeding by conventional methods, he cannot afford to divert part of his resources to mutation breeding".

24. The same conclusion seems appropriate in general for other highly specialized tools of breeding. There is so much to be done and the potentials for development by conventional plant breeding procedures are so great that efforts in the developing countries should be concentrated primarily on them.

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